The structure and robustness of an epiphyte - phorophyte commensalistic network in a neotropical inselberg

Abstract

Ecological networks describe the interactions between species, the underlying structure of communities, the function and stability of ecosystems. To date, network analyses have been extensively applied to understand mutualistic and antagonistic interactions, but few have examined commensal interactions, particularly in neotropical regions. The inselbergs of southeastern Brazil are considered one of the three most important regions in the world in terms of terrestrial species diversity and endemism but are poorly studied. In this study, we constructed the first epiphyte-phorophyte commensalistic network in a Brazilian inselberg and examined its structure and robustness to simulated species loss. A total of 138 phorophyte individuals belonging to eight species were observed in 20 2 m × 50 m transects, interacting with 5,039 individuals of vascular epiphytes belonging to 85 species. The epiphyte-phorophyte network structure exhibited a low degree of specilization (H_2'), low connectance and robustness; when the most connected phorophyte species were sequentially removed the number of secondary extinctions was high, based on robustness metrics. One generalist phorophyte, *Pseudobombax* sp. nov., was particularly important, hosting a high number of epiphyte species. A single phorophyte individual of *Pseudobombax* supported 46% of the total richness of the epiphyte community studied. Our results demonstrate that the richness and abundance of epiphytes were correlated with phorophyte size (as mensured by the DBH, diameter at breast height), probably due to increased habitat area and the time available for colonization. We conclude that phorophyte size and species identuty are important factors for predicting the structure of epiphyte-phorophyte interaction networks.

We discuss the conservation implications of phorophyte loss and secondary extinctions of epiphytes in Atlantic Forest inselbergs.

Key words: Atlantic Forest, biodiversity hotspot, conservation, facilitation, host tree

INTRODUCTION

In the Brazilian Atlantic Forest, there are granitoids rock outcrops ecosystems, named inselbergs (Porembski *et al.* 1998). They are very old, isolated landscapes that formed between 625 and 490 Ma ago (Gradim *et al.* 2014). These residual landforms are characteristic mainly of tropical and subtropical regions, although they occur across all continents (Porembski 2007; Hopper 2009; Couto *et al.* 2016; De Paula *et al.* 2016). In Brazil, they are considered one of the three global hot spots in terms of diversity and endemism of terrestrial plant species (Porembski 2007, De Paula *et al.* 2016). Due to their insular nature and unique combination abiotic factors, the inselbergs are ecologically characterized by a range of harsh conditions, such as high temperatures and radiation, and low water and nutrient contents in the soil (Barthlott *et al.* 1993). These characteristics promote the occurrence of high numbers of geographically restricted, specialized, and threatened species (Porembski & Barthlott 2000; Porembski 2007; De Paula *et al.* 2016; Couto *et al.* 2017), and their conservation is of global importance (Porembski *et al.* 2016). However, these ecosystems are threatened, mainly by quarrying, invasive grasses, tourism and extraction of ornamental plants, resulting in biodiversity loss and degradation of their ecosystem services (Galindo-Leal *et al.* 2003; De Paula *et al.* 2016; Porembski *et al.* 2016; Hopper 2009).

Although the flora of theses inselbergs is characterized mainly by herbs and shrubs (Porembski 2007; De Paula *et al.* 2016; Couto *et al.* 2017), rupicolous trees, even though

rarer in these environments, are important for the promotion of the diversity of these ecosystems and have received little attention (Yarranton & Morrison 1974; Couto *et al.* 2016). Increasing this knowledge would be a source of basic information for both conservation and restoration of these unique environments, because the removal of tree species are highly damaging to the epiphytic communities they support.

Vascular epiphytes are plants that germinate and live on other plants (phorophytes) during some stage of their life cycle (Benzing 1990). They are structurally dependent on phorophytes that provide substrate and a variety of environments with different microhabitats in a single tree (Sanger & Kirkpatrick 2016). Epiphytes use phorophytes (trees) only as structural support and establish a commensal relationship. Thus, epiphyte-phorophyte interactions represent a type of commensalistic network (Burns 2007). To date, network analyses have mostly focused on mutualistic interactions (e.g., plants and their pollinators and seed dispersers) (Bascompte *et al.* 2003; Evans *et al.* 2013; Mello *et al.* 2015) or antagonistic interactions (Thébault & Fontaine 2010; Bellay *et al.* 2015). By comparison, there are few studies of commensal interactions (Cockle & Martin 2015; Ceballos *et al*. 2016), particularly among epiphytes-phorophytes. This is possibly due to the logistical difficulties associated with the sampling of this group of plants in the forest canopy. This also makes species identification difficult and hampers complete inventories of the epiphytic flora. Few studies of epiphyte-phorophyte interactions have been conducted, all of them in tropical and subtropical (Silva *et al.* 2010; Zhao *et al.* 2015) and temperate forests (Burns 2007; Taylor *et al*. 2016). Further, some studies comprised low species richness communities (Burns 2007; Blick & Burns 2009; Ceballos *et al.* 2016) or considered only a subset of the existing epiphytic species, such as orchids (Silva *et al.* 2010) or bromeliads (Sáyago *et al.* 2013).

Ecological networks describe the interactions between species, the underlying structure of communities, the function and stability of ecosystems (Thébault & Fontaine 2010; Memmott *et al.* 2004). Network analyses of epiphyte-phorophyte interactions have found nested structures for different forests (Burns 2007; Sáyago *et al.* 2013; Ceballos *et al.* 2016). In a nested network, species with fewer interactions (specialists) are connected with species that have many interactions (generalists) (Bascompte *et al.* 2003). Epiphyte-phorophyte networks also exhibit low levels of specialization (Sáyago *et al.* 2013; Zhao *et al.* 2015; Ceballos *et al.* 2016; Taylor *et al.* 2016). This may result from the selection of epiphytes by specific phorophytes traits (Sáyago *et al.* 2013; Zhao *et al.* 2015; Ceballos *et al.* 2016) and several tree species may be appropriate phorophytes, reducing the vulnerability of epiphytes to perturbations. Thus, the complexity and structure of epiphytes-phorophytes networks have been in described few studies. However, to our knowledge, no study to date examined the tolerance of the network to species extinctions (Dunne *et al.* 2002; Memmott *et al.* 2004). The 'robustness' of a network is related to the tolerance of the network to species extinctions (Dunne *et al*. 2002; Memmott *et al.* 2004). In a commensalistic network, the robustness can be assessed by sequentially removing primary phorophyte species from the network and calculating the number of epiphyte secondary extinctions that occur as a result (Dunne *et al.* 2002; Memmott *et al.* 2004; Ings *et al.* 2008). Such an approach is useful in evaluating whether a network is particularly fragile to disturbance and can be used in ecosystem restoration (Pocock *et al.* 2012). Studies in different environments comparing epiphyte species richness show that phorophyte size is an important factor determining the diversity and abundance of vascular epiphytes (Flores-Palacios & García-Franco, 2006; Sáyago *et al.* 2013; Zhao *et al.* 2015; Wagner *et al.* 2015; Wang *et al.* 2016). Tree size is related with other tree characteristics such as increase in habitat area, greater microhabitat heterogeneity, tree architecture and bark structure (Zhao *et al.* 2015; Woods *et al.* 2015; Wang *et al.* 2016). The diameter at breast height

(DBH) has been used as proxy for age and size of phorophytes (Flores-Palacios & Garcia-Franco, 2006; Taylor *et al.* 2015; Zhao *et al.* 2015; Wang *et al.* 2016).

In this study, we investigated the network structure and robustness of an epiphyte-phorophyte commensalistic network in an inselberg in Southeastern Brazil, a tropical system of high ecological importance (Porembski 2007). We also evaluated how different weights of the links in the network can influence the structure of the system. Our expectation was that the network structure is nested, with a low degree of specialization, as found for the majority of the interaction networks involving vascular epiphytes. We used phorophyte diameter (represented by DBH) as a surrogate for phorophyte size and hypothesized that the size of the phorophyte is the best predictor of interaction frequencies and metrics of the vascular epiphyte-phorophytes network. Phorophyte size represents a number of aspects that affect vascular epiphyte richness and abundance, including mainly age (the time available for establishment of epiphytes) and surface area and microhabitats available for colonization of epiphytes (Zhao *et al.* 2015; Wang *et al.* 2016). Thus, we also investigated whether phorophyte size correlates with the richness and abundance of epiphyte species in the inselberg.

METHODS

Study site

The study was conducted in a montane granite-gneiss inselberg in the State of Espírito Santo, southeastern Brazil (20º56'19.94"S and 41º32'39.77"W), situated at 782 m of altitude (Fig. 1) in September 2015. This inselberg has an area of about 2.5 ha covered with rupestralvegetation growing on very shallow soils (litholic humic neosol) (Embrapa 2009), which at some points, shows a small layer of leaf litter, above a thicker layer of soil. The inselberg is well preserved and is inserted in a transition matrix between semi-deciduous

mountain forest, dense ombrophilous forest and anthropogenic areas, namely coffee plantations (*Coffea arabica* L.), grasslands and eucalyptus forests (Couto *et al.* 2016). Climate is Cwb (Köppen 1948) moderate humid subtropical, mesothermal humid, with rainy summers and dry winters.

Data collection and specimen vouchering

We sampled holoepiphytes (complete life cycle on host tree) and hemiepiphytes (with a life stage as terrestrial plants) and phorophytes in 20 linear transects of 50 m x 2 m distributed systematically at parallel intervals of 10 m and vertically at 5 m (Gentry 1982). This arrangement allowed us to maximize environmental variation in the sampling. All phorophytes (shrubs/trees) present in the transects with DBH (diameter at breast height) ≥ 5 cm were sampled.

For each phorophyte we recorded the presence and abundance of vascular epiphyte species. We counted all epiphyte stands to obtain abundance (Sanford 1968). Following Sanford (1968), we considered as a 'stand' a group of rosettes (Bromeliaceae), leaves (ferns, Gesneriaceae), or stems (Orchidaceae, Araceae, Cactaceae) of a single epiphyte species spatially separated from another group of the same species by a space in the tree devoid of epiphytes or occupied by another species.

The identification of vascular epiphytes occurring in the inselberg was based on Couto *et al*. (2016) with reference materials deposited in the herbarium of the Biology Museum Prof. Mello Leitão (Museu de Biologia Professor Mello Leitão - MBML) and in the herbarium of the Federal University of Espírito Santo (VIES). The nomenclature of the angiosperms (magnoliids, monocotyledons and eudicots) followed the suggestions of APG IV (The Angiosperm Phylogeny Group 2016) and ferns (monilophytes) following PPG I (The Pteridophyte Phylogeny Group 2016).

149 **Estimation of sampling completeness of interactions**

150 We plotted the number (richness) of accumulated interactions as sampling effort
151 increased for each phorophyte species to estimate network sampling completeness. We
152 adapted the methodology of Traveset *et al.* (2015) for each of the eight phorophyte species
153 from which more than five individuals were sampled. We calculated the asymptotic estimated
154 epiphyte richness (S_E) using the non-parametric diversity estimation Chao 2 (Chao 2005;
155 Gotelli & Colwell 2011). Posteriorly, we calculated the percentage of estimated asymptotic
156 richness detected (% S_{OBS}):

157 $$\% S_{OBS} = 100 * S_{OBS} / S_E$$

158 where S_{OBS} is the observed epiphytes richness in the samples (phorophytes linkage level) and
159 S_E is the epiphyte richness estimated with Chao 2. The Chao 2 estimator is based on species
160 presence / absence of data that quantifies rarity or the number of singletons (species that
161 appear in only one sample) and duplicates (species that occur in two samples). Chao 2 was
162 applied because it is the more robust estimator for small sample sizes (Chao *et al.* 2009).
163 Chao 2 was estimated using the R statistical software (R Development Core Team 2016) with
164 the 'vegan' package (Oksanen *et al.* 2016).
165
166 **Network analysis**

167 We examined the structure and complexity of the networks using standard metrics.
168 Connectance (*C*) consists of the actual number of observed interactions in relation to the
169 number of theoretically possible interactions in the network. It varies from 0 (without
170 interaction) to 1 (all species linked to each other) (Jordano 1987). We used the specialization
171 index (H_2'), to evaluate the network specialization (Blüthgen *et al.* 2006), by selectivity in the
172 use of resources of the whole network, which varies between 0 (full generalization) and 1
173 (full specialization). The significance of H_2' was estimated by randomization (1000

interations), using the Patefield null model (Blüthgen *et al.* 2006). Generality and vulnerability (Tylianakis *et al.* 2007) were also calculated to examine epiphyte-phorophyte interaction asymmetries. Generality is the weighted average number of phorophytes connected to epiphytes, and vulnerability estimates the epiphytes connected to phorophytes (Sáyago *et al.* 2013; Zhao *et al.* 2015).

We examined network nestedness by *NODF* (nested metric based on overlap and decreasing fill) (Almeida-Neto *et al.* 2008). For epiphyte-phorophyte networks, nestedness represents phorophyte species with low interactions forming a subset of species that maintains large numbers of interactions. It varies from 0 (non-nested) to 100 (fully nested) (Almeida-Neto & Ulrich 2011). We assessed nestedness significance using empirical values from the null distribution. For this, we calculated 1000 random matrices using the null model 2 (CE) proposed by Bascompte *et al.* (2003), producing a matrix of the same size and the same number of interactions as the one produced, and we tested the probability of an interaction occurring considering the number of occurrences in the rows and columns.

Robustness (*R*) was used to measure the tolerance of the network to species extinctions (Dunne *et al.* 2002; Memmott *et al.* 2004). Although sampling biases are likely to affect network-level analyses such as this, our aim was to provide the first measure of the 'fragility' of the networks for the region. Robustness was calculated by considering the secondary extinction of epiphytic species resulting from the extinction of primary species of phorophytes. $R \rightarrow 0$ corresponds to a very rapid reduction in the slope of the curve, reflecting a disturbed system after the first species is removed; whereas $R \rightarrow 1$ represents a very robust system, where decrease in the curve corresponds is very slow, and thus represents a system in which most epiphytes remain after the removal of most phorophytes. The community robustness was measured through the area below the extinction curve (Memmontt *et al.* 2004*;* Burgos *et al.* 2007), by sequentially deleting the most connected (generalist) to less

connected (specialists) phorophytes. Using this method, it is also possible to verify if the generalist species of phorophytes that are removed leads to the removal of the species of epiphytes that interact only with these hosts. It was generated from extinction curves through the function *second.extinct* (1000 randomizations).

All analyses were carried out using the function 'network level' from the 'bipartite' package (Dormann *et al.* 2008) in R statistical software (R Development Core Team 2016)., except for nestedness that was carried out using ANINHADO version 3.0.2 (Guimarães-Jr & Guimarães 2006).

Organization of interactions

The species' degree (*ki*) is defined by the number of interactions that each species has. In general, species with few interactions (i.e. species with low degree value) are usually referred to as specialists, whereas those that establish many interactions (high degree value) are regarded as generalists. The push/pull (PP) was calculated to characterize the direction of asymmetric interactions based on the dependencies of the species (Vázquez *et al.* 2007). This metric ranges from -1 to 1 and the closer to 1 the greater the dependence. Species strength (SS), suggested by Bascompte *et al.* (2006), has a high correlation with the degree of the species and is understood as the sum of the dependencies of the epiphyte species for a phorophyte species. The higher the value, the more generalized the phorophyte because more epiphyte species depend on it. Analyses were carried out using the function 'species level' from the 'bipartite' package (Dormann *et al.* 2008) in R statistical software (R Development Core Team 2016).

Other data analysis

Spearman's rank correlations were calculated to examine the relationships between the epiphyte richness and abundance and tree DBH. The data of DBH of phorophytes were compared using Kruskal-Wallis test, followed by multiple comparisons with *a posteriori* Dunn test (Zar, 2010). Differences were considered significant at $p < 0.05$. Analyzes were performed in R statistical software (R Development Core Team 2016).

RESULTS

Richness and diversity

138 phorophytes from eight species and eight families, hosted 5,039 individuals of vascular epiphytes from 85 species, 44 genera and 11 families (refer to Appendix S1 for the complete list of epiphyte species). The epiphytic families most represented were Orchidaceae (34 species, 40%), Bromeliaceae (22 species, 26%) and Polypodiaceae (8 species, 10%) (Fig. 2, Appendix S2).

The richness and abundance of epiphytes showed high correlation with the size of phorophytes. The richness of epiphytes increased significantly with DBH (Spearman's correlation; $r^2 = 0.64$, $p<0.001$), as did the abundance of epiphytes increased significantly with DBH (Spearman's correlation; $r^2 = 0.55$, $p<0.001$).

Network structure

Estimation of sampling completeness showed that the sampling effort was adequate. We detected a large proportion of all interactions for the whole epiphyte-phorophyte network (~ 80%) (Appendix S3). Variation in network structure across transects was low (Table 1). We found low specialization ($H_2' = 0.30$; $p<0.01$) between epiphytes and phorophytes, and low connectance ($C = 0.23$). Theoretically, 680 interactions between species of epiphytes and

247 phorophytes are possible, but only 156 interactions (23%) were recorded (Fig. 3, Appendix
248 S4). The species of epiphytes interacted on average with two species (2.05 species) of
249 phorophytes (generality), while the eight species of phorophytes interacted on average with
250 eighteen (18.01) species of epiphytes (vulnerability). The phorophyte-epiphyte network was
251 nested (*NODF* = 57.50; p<0.01), showing asymmetry in the interactions (Appendix S4). The
252 network exhibited low robustness (R = 0.21) (Fig. 4), meaning phorophyte-epiphyte
253 interactions are little tolerant and sensitive to perturbations, with potential implications for
254 extinction risk. For this commensalistic network, the loss of the most generalist phorophyte,
255 *Pseudobombax* sp. nov., promoted a very rapid reduction in the slope of the curve, reflecting
256 a disturbed system, leading to a local secondary extinction of approximately 45% of the
257 species of epiphytes (Fig. 4, Appendix S4). The removal of the second most generalist
258 phorophyte (*Guapira opposita*), although it is the most abundant phorophyte, caused little
259 impact on the network, since this phorophyte had few unique (occurring only in this
260 phorophyte) interactions.
261
262 **Organization of interactions**
263 The number of interactions (degree) for phorophyte species varied from 1 to 71
264 (Tables 2, Appendix S1). The phorophyte *Pseudobombax* sp. nov. showed the greatest
265 number of interactions in the network (71 species of epiphytes – 46% of 156 interactions)
266 (Fig. 3; Appendix S1). Of these, 38 (45%) were exclusive species for this phorophyte, being
267 16 (42%) species of Orchidaceae, eight (21%) species of Bromeliaceae, four (10%) species of
268 Araceae, four (10%) species of Polypodiaceae, two (5%) species of Aspleniaceae and one
269 (3%) species for Araliaceae, Begoniaceae, Cactaceae and Piperaceae. In addition,
270 *Pseudobombax* sp. nov. interacted with several endangered species (Appendix S2).
271 *Oreopanax capitatus* (ORCAP) interacted with one species of vascular epiphyte, *Billbergia*

horrida Regel, that was also present on *Pseudobombax* sp. nov. (PSSPN); *Guapira opposita* (GUOPP) and *Eugenia* cf. *longipedunculata* (EULON) (Fig. 3, Appendix S1). Five species of phorophytes, *Bactris* sp. (BASP), *Clusia arrudea* (CLARR), *Eremanthus crotonoides* (ERCRO), *Handroanthus* sp. (HASP) and *Oreopanax capitatus* interacted with one to nine species of epiphytes (Tables 2, Appendix S1).

Two species of phorophytes, *Pseudobombax* sp. nov. and *G. opposita*, interacted together, with almost 100% of the epiphytes recorded in this study (Fig. 3, Appendix S4). *Guapira opposita* was the most abundant phorophyte (88 individuals, 62%) (Appendix S5), followed by *Pseudobombax* sp. nov with 23 individuals (16%). *G. opoosita* interacted with 46 vascular epiphytes (Fig. 3, Appendix S4, S6), with nine exclusive species: *Billbergia tweedieana*, *Campylocentrum brachycarpum*, *Epidendrum campaccii*, *Gomesa recurva*, *Monstera adansonii*, *Pleopeltis squalida*, *Stelis argentata*, *Vriesea gigantea* and *Xylobium variegatum*, and two endangered species for the Espírito Santo state flora (*Acianthera saurocephala* and *Bulbophyllum cantagallense*) (Appendix S1, S2).

We observed that epiphytic richness per individual phorophyte varies from one (on *Oreopanax capitatus*) to 39 species (46%) recorded on a single individual *Pseudobombax* sp. nov. (Fig. 5). *Pseudobombax* sp nov. was the most generalist phorophyte species (degree = 71). When compared with all other phorophyte species, the dependence of epiphyte species in this phorophyte is evident (species strength = 58.7) and (push/pull = 0.8), strongly affecting the epiphytes in the interaction (Table 2). It was also the largest sized phorophyte with 117 cm of diameter. We found significant differences among the DBH species of phorophytes (Kruskal-Wallis: $H= 50.376$, $df = 7$, $p<0.05$), and *Pseudobombax* sp. nov. differed from all other species (Appendix S5).

The most important phorophytes for the epiphytic flora in the inselberg were *Pseudobombax* sp nov. and *Guapira opposita* which together interact with almost 100% of

297 epiphytes and exclusively interacted with 14 (16%) epiphytic species (Fig. 3, Appendix S4).
298 These phorophytes share 33 (39%) species of vascular epiphytes (Fig. S1). The other
299 phorophytes interacted largely with an epiphytic flora that were present in these two
300 phorophytes species (Fig. 3, Appendix S4).

301 The most abundant vascular epiphytes were *Tillandsia usneoides* (1,167 individuals,
302 23%) followed by *Tillandsia recurvata* (699 individuals, 14%), *T. tenuifolia* (543 individuals,
303 11%) and *Vriesea lubbersii* (392 individuals, 8%) (Appendix S2). All belong to the family
304 Bromeliaceae, subfamily Tillandsioideae. The epiphyte *T. usneoides* was the most generalist
305 (high vertex degree value; k = 7) species and occurred on seven of the eight species of
306 phorophytes (Fig. 3, Appendix S1).

307

308 **DISCUSSION**

309 The present study is, to our knowledge, the first to use ecological network analysis to
310 investigate the structure and complexity of epiphyte-phorophyte commensalistic interactions
311 in a Neotropical inselberg. We found a diverse epiphytic community, an unexpected feature
312 for this type of environment (see Porembski *et al.* 1998). Our results support the hypothesis
313 that phorophytes with larger dimensions would have greater diversity of epiphytes and are the
314 ones that most interact with them. In addition, we showed that phorophyte size, based on
315 DBH, is an important factor for predicting the structure of the epiphyte-phorophyte
316 interaction network. We found a nested pattern and low degree of specialization for the
317 network, as has been found for other epiphyte-phorophyte networks in forest ecosystems
318 (Burns 2007; Sáyago *et al.* 2013; Zhao *et al.* 2015). Generalist phorophytes that preserve
319 unique interactions with the epiphytes are those that maintain the robustness of the network.

320

Richness and diversity

The richness of vascular epiphytes in this study corroborates the data obtained by Couto *et al*. (2016) and showed relatively high richness recorded in studies that quantify the epiphytic flora in Brazilian rocky environments (Werneck & Espírito-Santo 2002; Conceição *et al.* 2007; Alves *et al.* 2008). This result certainly is related to the presence of large trees in the studied inselberg, such as some individuals of *Pseudobombax* sp. nov., that has crown branches with larger diameters and less inclination than the other phorophyte species. Moreover, the presence of exposed roots of considerable thickness on the rocky surface provides an important site for colonization by epiphytes (Couto *et al.* 2016).

As expected, we found a positive and significant correlation between richness and abundance of the epiphytic community with the size of phorophytes. The phorophyte size produces a complexity of ecological factors that are intimately related with the distribution of the epiphyte community. Large trees are usually older (Sáyago *et al.* 2013; Wang *et al.* 2016) and therefore they are exposed for a longer time to diaspore settlement events through seeds or plant parts (e.g., *Tillandsia usneoides*) (Callaway *et al.* 2002; Flores-Palacios & García-Franco 2006). This is due to the greater surface area exposed to receive the seed rain and for seedling establishment, the greater heterogeneity of microhabitat available, and the improvement in bark quality and larger exposition to air moisture and light (Woods *et al.* 2015; Zhao *et al.* 2015). These specific features of older phorophytes, in conjunction, are directly responsible for the greatest diversity and composition of epiphytic species in specific phorophytes (Krömer *et al.* 2007; Zhao *et al.* 2015; Woods *et al.* 2015; Ding *et al.* 2016). In contrast, small trees are generally young and have a small area available for colonization, with little variation in the environmental conditions (Woods *et al.* 2015; Wang *et al.* 2016). Exceptions can be observed for trees and shrubs from *campos rupestres*, where phorophyte size seems less important (Alves *et al*. 2008), as observed for arborescent genus *Vellozia*

(Velloziaceae). The phorophytes of this genus are small but known to live for several centuries (Alves 1994). They hosted epiphytic species considered restricted to the caudices of their species (see Porembski 2003; Alves *et al*. 2008; Menini Neto *et al*. 2013).

The vascular epiphyte families with highest richness in this study (Orchidaceae, Bromeliaceae and Polypodiaceae) are also the richest worldwide (Zotz 2013) and especially in neotropical regions (Gentry & Dodson 1987; Boelter *et al.* 2014; Freitas *et al.* 2016). These families have a wide distribution in ecosystems associated with the Brazilian Atlantic Forest (Couto *et al.* 2016; Freitas *et al.* 2016).

Network structure

The epiphyte-phorophyte network exhibited low connectance, degree of specialization and nested structure. High connectance can promote the persistence and resilience of mutualistic networks (Thébault & Fontaine 2010) and antagonistic networks (Dunne *et al.* 2002), but we found low connectance similar to many other antagonistic parasite-host networks (Bellay *et al.* 2015), mutualistic plant-pollinators networks (Blüthgen *et al*. 2006) and commensal networks (Ceballos *et al.* 2016). In this study, the low interaction recorded may be related to the rocky environment which does not favor the establishment of diverse and structured arboreal and shrubby strata, restricting the number of species with large phorophytic individuals (Porembski *et al.* 1998; Porembski & Barthlott 2000). Normally, these large individuals which are more appropriate to the establishment of epiphytic flora (Zhao *et al*. 2015; Wang *et al.* 2016).

There was a low degree of specialization in the use of phorophytes by the epiphytes. This is an expected pattern for structurally dependent plants, such as the epiphytes (Wagner *et al.* 2015; Ceballos *et al.* 2016). Ecological theory does not predict strong interactions between commensal species, which are generally established between epiphytic and phorophyte species (Burns 2007; Sáyago *et al.* 2013, Zotz 2016). In general, low specialization

371 demonstrates that the representativeness of the phorophytes occurs similarly among the
372 species of epiphytes. Two species of generalist phorophytes, *Pseudobombax* sp. nov. and *G.*
373 *opposita*, interacted with almost 100% of the epiphyte species recorded in this study. The
374 degree of specialization in commensal networks of epiphytes and phorophytes may be a
375 result of the preference of epiphytes for specific phorophytes traits (Sáyago *et al.* 2013;
376 Taylor *et al.* 2016). Although phorophyte specificity, the exclusive presence of one epiphyte
377 species on one phorophyte species, is uncommon (Alves *et al.* 2008; Porembski 2003; Menini
378 Neto *et al.* 2013), often some trees are better phorophytes for epiphytes than others (Laube &
379 Zotz 2006; Wyse & Burns 2011; Sanger & Kirkpatrick 2016) due to their structural
380 properties (e.g., as phorophyte size, inclination of the branches and bark type) (Wagner *et al.*
381 2015) or a combination of these factors (Sáyago *et al.* 2013; Boelter *et al*, 2014) which may
382 vary among individual trees according to age (Burns & Zotz 2010; Taylor & Burns 2015).
383 However, Callaway *et al.* (2002) and Wagner *et al.* (2015) suggested that epiphyte species
384 should show more evident phorophyte specificity in habitats where climatic conditions are
385 suboptimal for their performance, like rocky outcrops. These habitats have low diversity of
386 potential phorophytes and low abundance of non-vascular epiphytes (such as mosses) and
387 phorophyte specificity is more evident (see Wagner *et al.* 2015).
388 The specific environmental characteristics present in the study area, (see Porembski
389 2007; Hopper 2009), may favor the existing asymmetry between the interactions of epiphyte
390 and phorophyte species. Here, we found that many epiphytic species were connected to few
391 phorophyte species (generality = 2.05). Nevertheless, the phorophytes were associated with a
392 lot more epiphytes species (vulnerability = 18.01) on average. The low value of generality
393 (2.05) differs from that found in other studies of epiphyte-phorophyte networks in tropical
394 forests (8.8 in Sáyago *et al.* 2013; 7.2 in Zhao *et al.* 2015; 8.47 in Ceballos *et al.* 2016).
395 Tropical forests are highly homogenous at regional scales, favoring the presence of more

phorophytes, and providing a greater variety of habitats for epiphytes from the trunk base (including the understory trees and shrubs) to the upper crown (Krömer *et al.* 2007; Zhao *et al.* 2015). Consequently, the epiphytes interact with a greater number of phorophytes (Zhao *et al.* 2015; Ceballos *et al.* 2016).

The epiphyte-phorophyte network showed a nested structure. This pattern is commonly associated with mutualistic interaction networks (Jordano 1987; Bascompte *et al.* 2003; Campbell *et al.* 2015). The same was recently found in commensalistic networks of cavity-vertebrate nesters (Cockle & Martin 2015) and for phorophytes-epiphyte in forest environments (Burns 2007; Silva *et al.* 2010; Sáyago *et al.* 2013; Ceballos *et al.* 2016). These findings and suggest that network size, vascular epiphyte succession, species abundance and phorophytes traits are important. We found that the phorophyte species with low interactions were also the phorophytes that had smaller diameters and hosted epiphyte communities that are subsets of the communities found in larger phorophytes, which showed higher interactions. Zhao *et al.* (2015) for montane tropical forests in southeastern China reported a similar result. Specialist epiphytes can only occur in older larger host trees (Burns 2007), contributing then to the nested pattern. *Pseudobombax* sp. nov. has a high diversity of specialist epiphytes, and other phorophytes have an epiphytic flora that derive from this phorophyte, leading the epiphyte-phorophyte interaction to a nested pattern. However, another factor that can contribute to the nestedness is a sequential colonization by epiphytes; so that pioneer species are beneficial to the specialist epiphytes species (see Burns 2007; Silva *et al.* 2010; Ceballos *et al.* 2016). Nevertheless, in our study it was not possible to observe this event.

The studied community appeared to be a fragile, sensitive to disturbance system. The removal of the more generalist phorophyte specie, *Pseudobombax* sp. nov, can rapidly lead to a collapse in the system, lowering diversity due to the secondary extinctions of many

epiphytes. *Pseudobombax* sp. nov. had many unique interactions in the network, as 45% of species of the epiphytes species occurred exclusively on this phorophyte. Many of such epiphytes are listed as threatened with some risk of extinction (e.g., *Barbosella spiritusanctensis* - Orchidaceae and *Oreopanix capitatus* - Araliaceae). This pattern was also found with antagonist networks, predator-prey (Dunne *et al.* 2002), host-parasite (Solé & Montoya 2001), and mutualistic plant–ant networks (Barriga *et al.* 2015). In the same way as to food webs (Dunne *et al.* 2002) the loss of highly connected species has serious consequences for the persistence of the network. Nevertheless, removal of specialist species (with few interactions) usually has little effect on the network structure (Dunne *et al.* 2002). Here, the extinction of specialist species as *Oreopanix capitatus, Bactris* sp., *Eremanthus crotonoides* and *Clusia arrudea* caused little impact on the secondary extinction of epiphytes. This was because these phorophytes do not have unique interactions and host an epiphytic flora that was present mainly in *Pseudobombax* and *Guapira opposita*. Therefore, the way species are removed from the network may affect communities in different ways, and this is related to the nature of the interaction among the removed species (Solé & Montoya 2001). . These results show the importance of the identification and protection of highly connected species. They play an important role in maintaining the richness and robustness of the network and should receive special attention in the conservation of the ecological processes that maintain diversity (Solé & Montoya 2001; Memmott *et al.* 2004).

The inselberg flora is naturally fragile (Martinelli 2007, Hopper 2009; Porembski *et al.* 2016). The resilience of this type of environment is very low compared to the surrounding ecosystems (Hopper *et al.* 2009), mainly due to its very restrictive environmental filters that select a very specific and endemic flora in each rock outcrop or specific region. In forest ecosystems, removal of important phorophytes leads to the significant loss of local epiphytic diversity (see Obermulle *et al.* 2012). The turnover of these large phorophytes by others

446 would probably take many years, even with highly diverse tree communities. The
447 *Pseudobombax* species is, to our knowledge, the main phorophyte kind of rocky areas of the
448 Atlantic Forest and replace it does not seem to be that simple. The inselbergs in the Brazilian
449 Atlantic Forest are exposed to a number of threats, ranging from the loss and fragmentation
450 of marginal habitats (Galindo-Leal *et al.* 2003), by quarrying (Martinelli 2007; Couto *et al.*
451 2016), by the invasion by exotic species (Martinelli 2007, De Paula *et al.* 2016; Couto *et al.*
452 2017) and indiscriminate collection of species for horticultural purposes (e.g. attractive giant
453 bromeliads, such the genus *Alcantarea* (Versieux & Wanderley 2015; some orchids as
454 *Aspasia lunata* and *Encyclia patens*; ferns and araceaes).
455
456 **Organization of the species**
457
458 As already presented by other authors who studied rocky ecosystems (Werneck &
459 Espírito-Santo 2002; Alves *et al.* 2008), phorophytes with low longevity (*e.g. Eremanthus*
460 *erythropappus* (DC.) MacLeish, *Hyptinodendron asperrimum* (Spreng.) Harley and *Myrsine*
461 *monticola* Mart.) supported the lowest richness of epiphytes. We observed that individuals
462 of *Eremanthus crotonoides*, a phorophyte with low longevity, hosted few epiphytes. These
463 were usually two species of wide geographic distribution: *Tillandsia usneioides* and *T.*
464 *gardneri* (Zotz 2013). Longer-lived trees, *Guapira opposita* and *Pseudobombax* sp. nov.,
465 hosted many others epiphytes species, such as Orchids, Bromeliads and Aroids.
466 In this study, an individual of *Pseudobombax* sp. nov. (9 m in height and 117 cm of
467 the DBH), hosted the highest species richness (39 species). Thus, the richness for epiphytes
468 on individuals of phorophytes was intermediate, considering the absolute values of richness,
469 as compared with other studies in tropical forest environments (21 species in Kersten &

Silva 2001; 30 in Kersten *et al.* 2009; 83 in Krömer *et al.* 2005; 126 in Schuettpelz & Trapnell 2006; 50 in Zotz & Schultz 2008).

In conclusion, we observed that generalist phorophytes, such as *Pseudobombax* play an important role in maintaining the richness and robustness of the network. This species needs to receive protection in conservation and restoration activities to prevent secondary extinctions, especially in these fragile inselbergs ecosystems., We propose that future research should address changes in inselberg network structure in space and time and even include other types of interactions, such as herbivory.

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686 **Tables**
687

688 **Table 1.** Mean and standard error (n = 20) of network metrics of interactions between vascular
689 epiphytes and phorophytes on a montane inselberg, Espírito Santo state, Brazil. H_2':
690 characterizes the degree of specialization and *NODF* (nestedness metric based on overlap and
691 decreasing fill) see methods.
692

Metrics	**Mean (±standard error)**
Connectance	0.53±0.02
H_2'	0.47±0.04
Generality	1.53±0.08
Vulnerability	6.57±1.03
NODF	41.41±3.55

693

694 **Table 2.** Observed values of species strength (SS), push/pull and degree of the eight species
695 phorophytes in the network commensal phorophyte and epiphyte recorded on a montane
696 inselberg, Espírito Santo state, Brazil.
697

Phorophytes species	**Code**	**Species strength**	**Push pull**	**Degree (k)**
Pseudobombax sp. nov.	PSSPNOV	57.68	0.80	71
Guapira opposita (Vell.) Reitz	GUOPP	22.52	0.47	46
Clusia arrudea Planch. & Triana ex Engl.	CLARR	0.34	-0.07	9
Eugenia cf. *longipedunculata* Nied.	EULON	4.27	0.17	19
Eremanthus crotonoides (DC.) Sch. Bip.	ERCRO	0.06	-0.47	2
Handroanthus sp.	HASP	0.09	-0.15	6
Bactris sp.	BASP	0.01	-0.49	2
Oreopanax capitatus (Jacq.) Decne. & Planch	ORCAP	0.02	-0.98	1

Figure captions

Fig. 1. (A) Study area in Espírito Santo state, southeast Brazil. (B) Note the presence of litholic neosoil, shallow and a vegetation arboreal-shrub sparse, without the formation of a continuous canopy in much of the inselberg and predominance of typical elements of inserlbegs south-american, as *Alcantarea* (Bromeliaceae). (C) *Pseudobombax* sp. nov.

Fig. 2. Diversity of the main epiphytic families registered on a montane inselberg, Espírito Santo state, Brazil.

Fig. 3. Network illustrating the interactions between epiphytes and phorophytes on a montane inselberg, Espírito Santo state, Brazil. Bars represent the species of epiphytes (on top) and phorophytes (bottom). The line width represent the observed interactions between the pairs (thicker line show greater interaction strength).(To identify the name of each species present in the network, see Table S1).

Fig. 4. Simulation of network robustness after removing of the most connected species of phorophytes to less connected in the network (by degree method) (Memmontt *et al*. 2004) phorophyte and epiphyte commensal interaction on a montane inselberg, Espírito Santo state, Brazil.

Fig. 5. Richness of species (A) and abundance (B) of vascular epiphytes by phorophytes species on a montane inselberg, Espírito Santo state, Brazil. The black horizontal bar represents the median and the lines above and below represent the first and third quartile, in that order.

Appendix

Appendix S1. List of vascular epiphytes, their interaction with each phorophyte present in the studied network and total number of interactions (degree (k)) on a montane inselberg, Espírito Santo state, Brazil. The color in rows indicates the interaction. Code of species phorophytes: PSSPNOV (*Pseudobombax* sp. nov.); GUOPP (*Guapira opposita* (Vell.) Reitz); EULON (*Eugenia* cf. *longipedunculata* Nied.); CLARR (*Clusia arrudea* Planch. & Triana ex Engl.); HASP (*Handroanthus* sp.); BASP (*Bactris* sp.); ERCRO (*Eremanthus crotonoides* (DC.) Sch. Bip.); ORCAP (*Oreopanax capitatus* (Jacq.) Decne. & Planch.).

Appendix S2. List of 85 vascular epiphytes, 44 genera distributed in 11 families showing the number of individuals and the number of colonized phorophytes on a montane inselberg, Espirito Santo state, Brazil. In front of the names of the families, the numbers of genera and species are shown in parenthesis.

Appendix S3. Estimation of sampling completeness of interactions analyses for each phorophyte species from which more than five individuals were sampled. S_{obs}: number of interactions observed; Chao S (Chao2 estimator) (see methods); N: number of individuals

sampled of each species. Detection: the proportion of interactions observed out of all those that are expected. For the name of each phorophyte species see Table S1, this section.

Appendix S4. Phorophyte-epiphyte interaction matrix on a montane inselberg, Espírito Santo state, Brazil. Species are ordered, in rows (phorophytes) of larger size species for smaller species (DBH) and columns (epiphytes) form the most generalized to the most specializes. Black cells indicate presence of interactions. Identify the name of each phorophyte and epiphyte species see Table S1, this section.

Appendix S5. Tree species sampled on a montane inselberg, Espirito Santo state, Brazil, followed by No (number of phorophytes individuals); Trans (occurrence of species in transects), DA (absolute density); DR (relative density); FA (absolute frequency in transects); FR (relative frequency in transects). Data are means ± SD (standard deviation): Basal area; DBH (diameter at breast height); Total tree height; Height trunk (height until the first inversion for the primary branches) and Number of primary branches. For each species, different letters indicate significantly different in the DBH (Dunn test: $P < 0.05$).

Appendix S6. Species richness of epiphytes present in each phorophytes species on a montane inselberg, Espirito Santo state, Brazil. The bars represent the species richness (number of species for each phorophytes) and the numbers above each bar corresponds to the abundance of epiphytes. PSSPNOV: *Pseudobombax* sp. nov.; GUOPP: *Guapira opposita*; EULON: *Eugenia* cf. *longipedunculata*; CLARR: *Clusia arrudea*; HASP; *Handroanthus* sp.; BASP: *Bactris* sp.; ERCRO: *Eremanthus crotonoides*; ORCAP *Oreopanax capitatus*.

References Appendix

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